Alytes, 1997, **15** (1): 26-36.

Microanatomy of the buccal apparatus and oral cavity of *Hyla minuta* Peters, 1872 larvae (Anura, Hylidae), with data on feeding habits

Dinorah D. ECHEVERRÍA

Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Biológicas, Laboratorio de Vertebrados, Universidad de Buenos Aires, 1428 Buenos Aires, Argentina

Histological and SEM observations of the buccal structures and reduced mouthparts of the tadpole of *Hyla minuta* revealed new anatomical features. There are few columns of cells that produce labial teeth in rows A-1 and P-2, and each column has only a few cells that produce teeth. The labial teeth are lightly pigmented, short and with 3-5 short cusps. Tooth development seems to be abbreviated and not continuous during ontogeny.

Tooth densities vary among rows, and tooth rows A-1, P-1 and P-2 may be incomplete or A-1 and P-2 may be absent. The number of conical cells in different stages of keratinization in the cellular columns of the jaw sheaths also varies.

Buccal roof arena papillae are sparse and tall, there are no lingual papillae, the ventral velum has reduced marginal projections, median and lateral ridges are present, and there are secretory pits on the dorsal velum and posterior buccal roof. Based on intestinal contents (i.e., periphytic algae, pieces of filamentous algae and cyperaceous plants including meristematic tissue, and free starch granules), these tadpoles have a broad, herbivorous macrophagous diet that appears to be harvested primarily by the jaw sheaths.

INTRODUCTION

The oral apparatus of anuran larvae usually consists of an oral disc with keratinized jaw sheaths and labial teeth positioned on transverse tooth ridges. The jaw sheaths are usually strongly pigmented and have a serrated edge, and labial teeth usually have cusps on the head. Histological features (e. g., *Alytes obstetricans*: BEAUMONT & DEUNFF, 1959; BOURGES & BACHELERIE, 1974, *Discoglossus pictus*: DEUNFF & BEAUMONT, 1959; *Rana pipiens*: CHENG, 1964, fide KUANG, 1975, LUCKENBILL, 1965) and development of these mouthparts (e.g., *Rana pipiens*: LUCKENBILL, 1965; KUANG, 1975; *Bufo arenarum*: FIORITO DE LOPEZ & ECHEVERRÍA, 1984, 1989) have been reported for a number of species with a labial tooth row formula of 2/3. This formula is extremely common in anuran tadpoles in many taxa and several ecomorphological guilds (ALTIG & JOHNSTON, 1989), but there are two general patterns that deviate from the norm: increases in tooth row number in lotic

tadpoles and decreases in tooth rows in several groups. Tooth row reductions accompanied by various other modifications of the oral apparatus are assumed to have occurred independently in four groups of small South American *Hyla*: *leucophyllata*, *microcephala*, *minuta* and *parviceps*. The pattern of reduction also varies among groups. *Hyla microps* larvae have neither labial ridges nor labial teeth (HEYER et al., 1990). In *Hyla nana*, labial teeth are absent, and the mouth is modified into a tube (LAVILLA, 1990). *Hyla sarayacuensis* tadpoles have labial ridges but lack teeth (ALTIG & JOHNSTON, 1989).

In an attempt to supply the comparative morphological information required to evaluate the assumption that tooth row reductions reflect a change in feeding mode compared with more typical tadpoles, I report the oral and buccopharyngeal anatomy of the tadpole of *Hyla minuta*.

MATERIAL AND METHODS

Hyla minuta tadpoles were obtained from semipermanent pools (maximum depth 40 cm) with rooted vegetation near the Iguazú River, Iguazú National Park, Provincia Misiones, Argentina. Samples were obtained from April to December (autumn to summer) in 1989-1993. Some tadpoles were reared through metamorphosis and preserved (SBM 38) to ascertain identification. Ten tadpoles were examined histologically, eight were observed with SEM, and two were dissected for camera lucida drawings. All specimens (stages 25-39) were staged by the table of GOSNER (1960), preserved in 10 % formalin when they were captured, and stored in the dark in 5 % formalin.

For light microscopy, the tadpole body was dehydrated, cleared, and embedded in paraffin (56-58°C), and serial sagittal and longitudinal sections cut at 4 and 7 µm were stained with Masson's trichrome (MARTOJA & MARTOJA-PIERSON, 1970). For scanning electron microscopy, the oral disc and buccal structures were critical-point dried and coated with gold-palladium. These specimens also were drawn with a camera lucida, and a video recording of some of the SEM observations is kept in the MEB-VIDEO (1993-94) collection. Lengths of labial tooth rows P-1 and P-2 were taken in conjunction with the SEM observation, according to ECHEVERRÍA's (1992) proposal. Drawings of the buccal structures were made with a camera lucida from specimens in stages 30 and 37.

Terminology follows ALTIG (1970) and DEUNFF & BEAUMONT (1959) for oral disc and tooth features, and VIERTEL (1982) for internal oral features. The descriptions of the histological features are based on FIORITO DE LOPEZ & ECHEVERRÍA (1989).

Pieces of the anterior intestine were dissected from two specimens at stages 25 and 32 for qualitative examination of the intestinal content by histological sections and with SEM.

Results

SEM observations

The oral disc has a single row of large marginal papillae along the lateral and ventral sides, and submarginal papillae are absent (fig. 1A). There are one upper and two lower labial ridges, and teeth are present on P-1 but often absent in A-1 and P-2. Row P-1 extends almost across the transverse diameter of the disc, but teeth in P-2 are frequently restricted to the medial area. If teeth are present in row A-1, the labial teeth are less dense (ca. 10-15 µm apart) than in P-1 and P-2. Individual teeth have a short head and no neck with modal total lengths of 15 µm and modal widths of 9 µm in P-1. There are 3 or 5 short, sharp, sharply angled cusps on each tooth, and the short sheath is tightly anchored to the soft tissue of the tooth ridge. In different rows (A-1 and P-1) and in different clutches, labial teeth morphology may vary (figs. 1B-C). The wide jaw sheaths have regular, conical serrations on the cutting edge (figs. 1A, D). The total modal length of these serrations is 20 µm, and modal width is 15 µm.

Buccal floor and roof features (figs. 2A-B)

The floor of the buccal cavity is triangular, and the branchial traps beneath the buccal floor are not evident. Two infralabial papillae (IP) present behind the jaw sheath are compressed and have a flat base and low projections on the free edge. Between these, a pair of prelingual papillae arranged in a transverse row have a rugose or slightly denticulate edge (fig. 3). The tongue anlage is large and lingual papillae are absent. The buccal floor arena is very broad but not well defined and has a densely pustulate surface, and no lateral papillae outline the arena. The complex prepocket papillae arise from a common base, and the obliquely oriented buccal pockets are ovoid with the long axis directed anteromedially. There are 1-2 pairs of medial projections on the posterior edge of the velum, and large secretory pits occur along the velum.

The roof of the buccal cavity is shaped like an equilateral triangle. The large, elongate internal nares are oriented obliquely, and the walls have a smooth narial valve. Postnarial papillae are absent. The postnarial arena contains (stages 25-36) a triangular pre-median ridge with three primary projections; the middle one is the largest (fig. 4A). By stage 37, this ridge is shaped like an inverted V (fig. 2B). Pustulations are present in the postnarial arena, and the lateral ridge is composed of a pair of long, simple and conical papillae. The anterior papillae have smooth or rugose edges, and the posterior ones are the tallest and are compressed laterally.

The triangular or crescent-shaped median ridge has small projections medially, and the poorly defined buccal roof arena has a dense field of pustules and a pair of long, conical, smooth marginal arena papillae on the posterior side of the arena. The glandular zone is straight, transverse, and bears secretory pits. The dorsal velum and marginal projections are absent (fig. 4B).

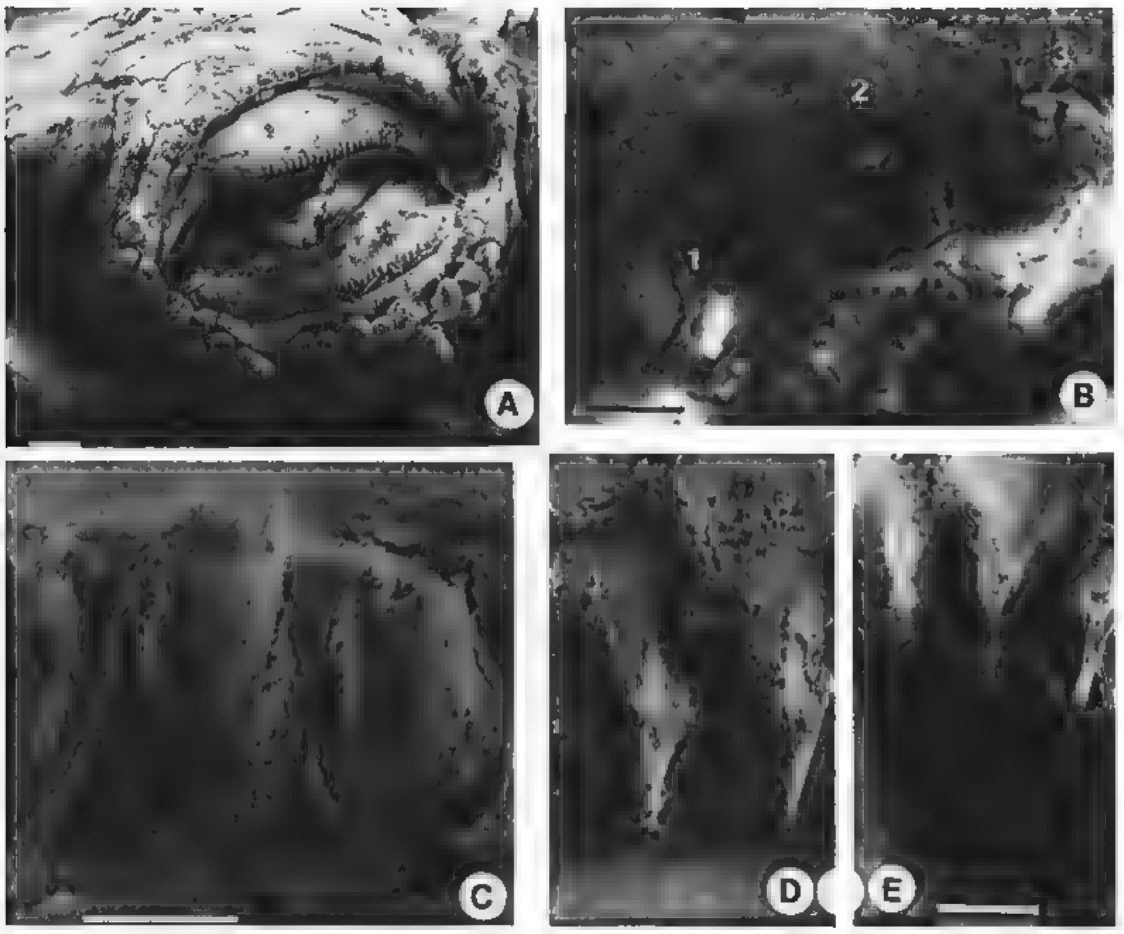

FIG. 1.— (A) SEM micrograph of the oral apparatus of *Hyla minuta*, stage 25. Scale line 100 µm. (B) Three labial teeth (1, 2, 3) emerging in row A-1, stage 25. Scale line: 10 µm. (C) Labial teeth of row P-1, stage 25 Scale line: 10 µm (D) Front view of upper jaw serrations, stage 25 (E) Rear view of same as in (D). Scale line: 10 µm.

LIGHT MICROSCOPE OBSERVATIONS

Sagittal sections show that the lower jaw sheath is longer than wide, and the infrarostral cartilage is subcircular in section. The suprarostral cartilage is long and narrow, and the upper jaw sheath is deeply convex and thicker than the lower sheath (fig. 5A). The upper and lower jaw cartilages are covered with a modified stratified epithelial tissue that gives rise to the cells that form the jaw sheaths. The core of the epithelium consists of several rows of cellular columns that contain several morphological cell types (figs. 5B-C): basal columnar cells lying over the basal membrane, flattened precone cells with basophilic cytoplasm, and cone cells in different stages of progressive keratinization from the proximal to distal end of the column. A layer of stratified epithelial tissue forms the oral (internal side) and labial (external side) surfaces of the sheath. When the jaw sheaths are closed, the edge of the lower jaw fits against the inner curvature of the upper jaw.

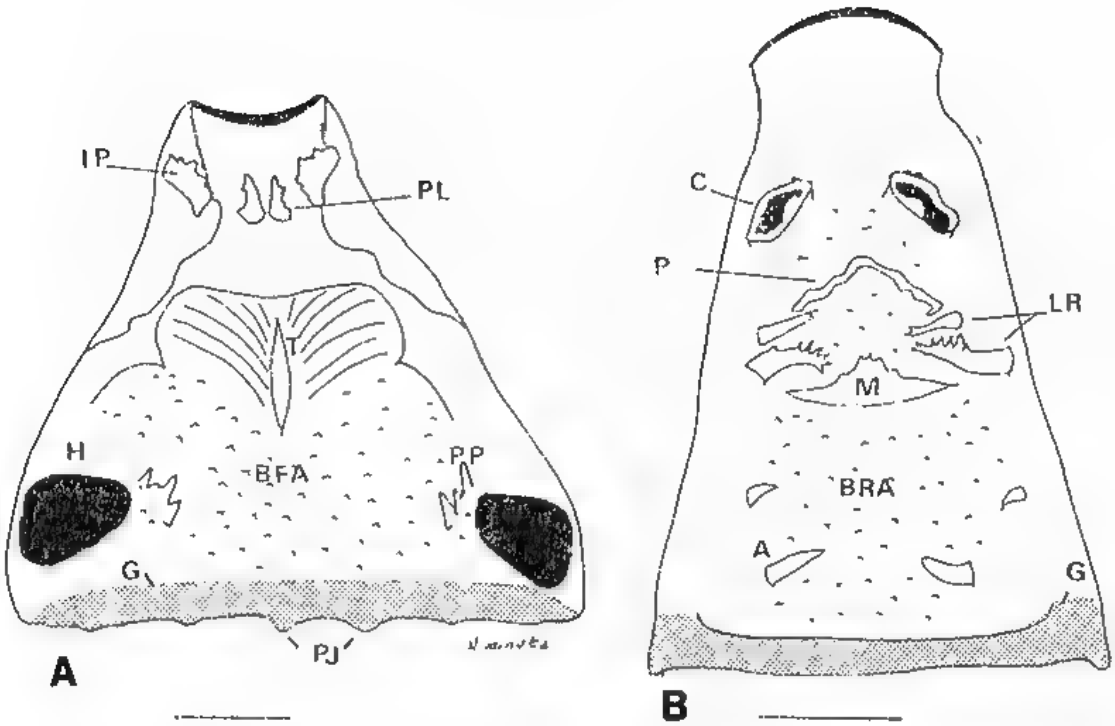

Fig. 2. – Camera lucida drawings of the (A) floor and (B) roof of the oral cavity, stage 37. A: marginal arena papilla; BRA: buccal roof arena; BFA: buccal floor arena; C: choana; G: area of secretory pits; H: buccal pocket; IP: infralabial papillae; LR lateral ridge; M: median ridge; P: pre-median ridge, PJ: projections; PL: prelingual papillae; PP: prepocket papillae, T. tongue anlage. Scale line: 500 µm.

There is one upper and two lower labial tooth ridges with a modified stratified epithelium. The columns of cells that develop teeth are positioned in the core of this epithelium (fig. 5D). The sequence of cells from the base of a tooth ridge to the top is as follows. basal column cells near the basal membrane, cylindrical odontoid cells with a cornified distal edge, 1-3 cells in different stages of keratinization and pigmentation, and 1-4 labial teeth. Few cells occur in the columns for rows A-1 and P-2 and these may be absent (figs 5C-D) The external and apical surface of the tooth ridge for A-1 is covered by a stratified epithelium (3-4 layers) that continues backwards as a bistratified epithelium. The inner and external faces of the posterior labial ridges are covered by stratified epithelium.

Remains of macrophytes of the family Cyperaceae and pieces of filamentous green algae were found in the intestine (figs 6A-B). Starch grains typical of macrophytes were seen in the histological preparations observed with polarized light, and diatom frustules were also found.

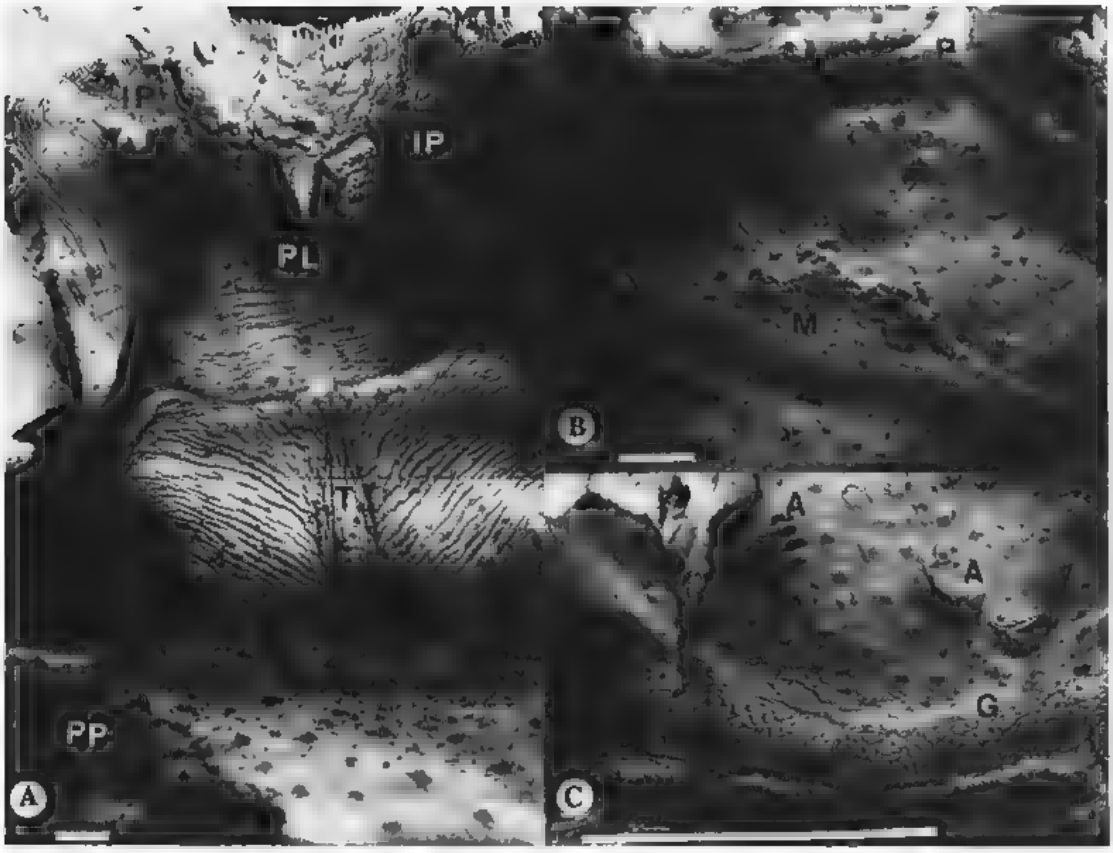

Fig. 3. – (A) SEM micrograph of the floor of the oral cavity, stage 30. Scale line: 100 µm. (B) SEM micrograph of the median ridge and pre-median ridge of the buccal roof, stage 30. Scale line: 100 µm (C) Glandular zone of the posterior part of the buccal roof, stage 30. Scale line: 1000 µm. A: buccal roof arena papilla; G: glandular zone; IP: infralabial papilla; M. median ridge, P: pre-median ridge, PL prelingual papilla; PP pre-pocket papillae; T: tongue anlage.

DISCUSSION

Labial tooth histogenesis in *Hyla minuta* occurs in the same pattern as in other species (e.g., *Bufo arenarum* and *Rana pipiens*), but the final result is different in each row. During the development of *B. arenarum*, histogenesis of the jaw sheaths and labial tooth is continuous (FIORITO DE LOPEZ & ECHEVERRÍA, 1989). The spatial sequence of the cells in each column in the sheaths of *Rana pipiens* represents a chronological sequence by their differentiation from basal epithelial cells (LUCKENBILL, 1965). In *Hyla minuta* the jaw sheath column cells are similar in size to those in *R. pipiens* and *B. arenarum*, but when labial ridge column cells of *Hyla minuta* are compared with those of *B. arenarum*, several differences are evident at the same stages. Labial ridge columns are shorter in *Hyla minuta* and component cells are not produced continuously throughout the larval period. The labial tooth columns of *H minuta* also differ from those of *B. arenarum* by the

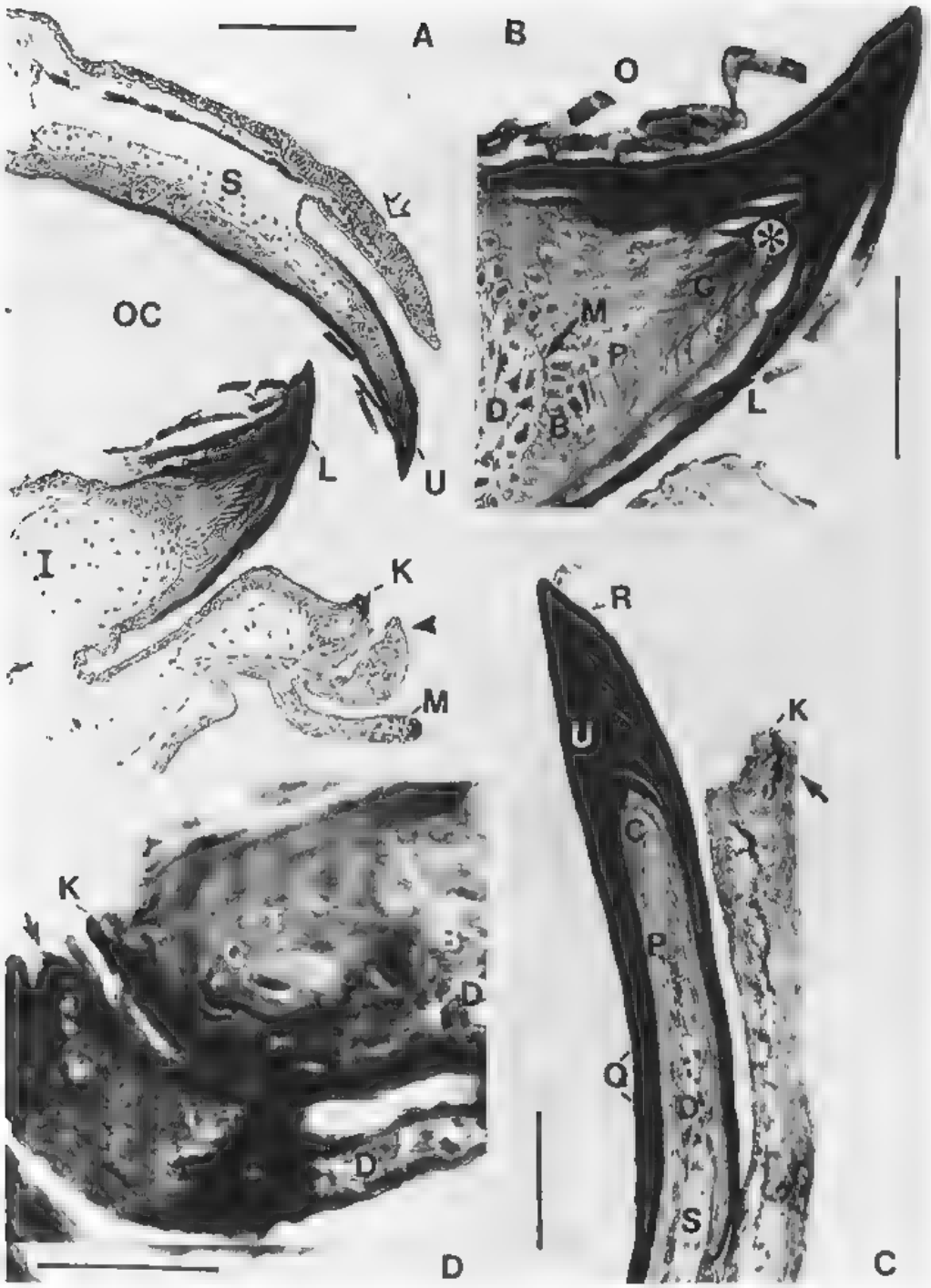

Fig. 4 — (A) Sagittal section of the buccal apparatus, stage 32. Scale line: 100 µm. Closed arrowhead, second lower tooth ridge, open arrow first upper labial ridge, I: infralabial cartilage; K: labial tooth; L: labial surface of lower jaw sheath; M: marginal papilla; OC: buccal cavity; S, suprarostral cartilage, U, upper jaw sheath (B) Sagittal section of lower jaw sheath, stage 32. Scale line: 100 µm. Asterisk: column of tooth cells in process of keratinization; B, basal cells; C cone cells, D dermis; O: oral surface of lower jaw sheath; P: precone cells. (C) Sagittal section of the (U) upper jaw sheath and (arrow) A-1 labial ridge, stage 32. Scale line: 50 µm. C: cone cells; D: dermis; K: labial tooth; P: precone cells; Q: keratinized oral surface of upper jaw sheath, R jaw serration, S: suprarostral cartilage. (D) Transverse section of (K) P-1 with labial teeth and (arrow) P-2 labial ridge with a tooth emerging, stage 32. Scale line: 30 µm. B basal cells; C. keratinization; D: dermis; T: odontoid cell.

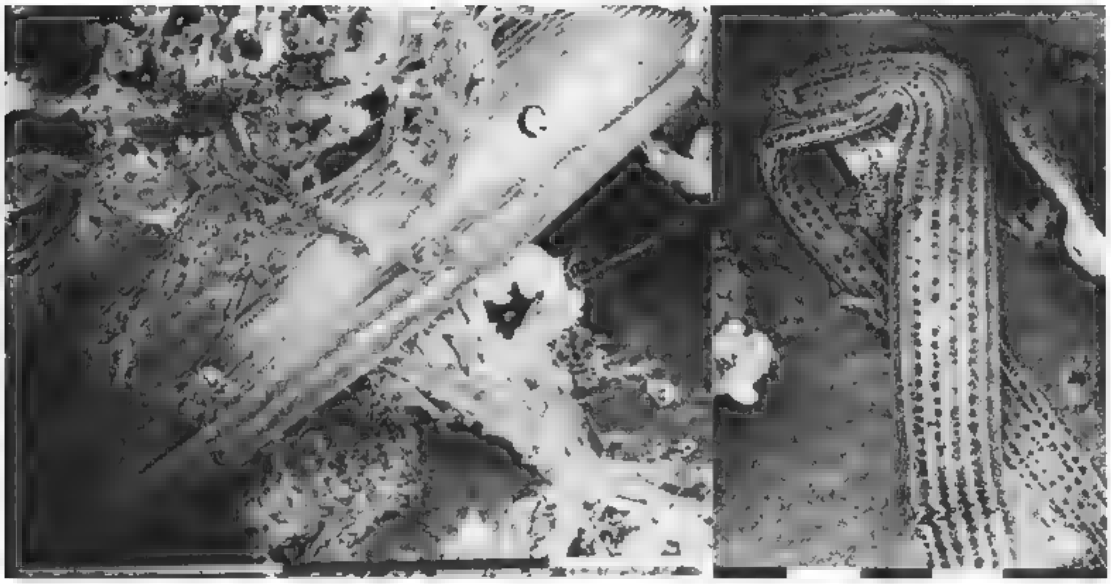

Fig. 5. – SEM micrographs of intestinal contents showing (A) a piece of a cyperaceous plant (C; scale bar: 0 1. mm) and (B) a piece of a filamentous alga (scale bar: 10 µm).

discontinuity of the column, and the morphological cell types forming each column are less evident than in *B. arenarum*. The distance between column cells differs according to the row being examined.

Compared with oral histogenesis of other species (LUCKENBILL 1965; FIORITO DE LOPEZ & ECHEVERRÍA, 1989), the formation of labial teeth in *Hyla minuta* is short-lived, especially in row A-1. Within these differences, the order of appearance of the tooth rows does not seem to fit the general pattern of appearance of the tooth rows that THIBAUDEAU & ALTIG (1988) proposed for 2/3 formulas. In *H. minuta* tadpoles at stage 25, P-1 may be the only row, but labial tooth row formulas of 0/1, 1/1 and 1/2 have been reported for specimens from Iguazú National Park (see also BOKERMANN, 1963; CEI, 1980; HEYER et al., 1990; MONTANELLI, 1991; KAPLAN, 1994), and DUELLMAN (1978) reported 0/2 for a population from Ecuador. It is possible to find more than one labial tooth row formula in certain species at the same stage, but tooth density and distribution usually do not change very much among specimens at the same stage and row (ECHEVERRÍA et al., 1987) *Hyla crucifer* has few teeth in P-3, and up to 50 % of the tadpoles may normally have a formula 2/2 instead of 2/3 (GOSNER & BLACK, 1957). BRESLER (1954) reported that abnormalities of labial teeth and jaw sheaths occurred in tadpoles of *Rana berlandieri* and in *Bufo cognatus* more frequently at higher developmental temperatures; spotty distributions and absences of teeth and jaw sheaths also occur. This is not the case in *H. minuta*, and the situation in this species may represent a polymorphism.

Hylid tadpoles have 0, 2 or 4 lingual papillae (WASSERSUG, 1980; LAVILLA & FABREZI, 1987; HERO, 1990; HEYER et al., 1990; ECHEVERRÍA & MONTANELLI, 1992) Hylid tadpoles that lack lingual papillae (including *Hyla minuta*) include some tadpoles with labial teeth reduced or absent: e.g., *Hyla ebraccata*, *H. sarayacuensis*, *H. mixe*, *H. microps*, *H.*

microcephala (WASSERSUG, 1980) and some non-feeding tadpoles (WASSERSUG & DUELLMAN, 1984). *Hyla minuta* tadpoles share some of the larval features found in *H. sarayacuensis* (*H. leucophyllata* group). few teeth, reduction of oral papillation and roof and floor arena papillae, and absence of lingual papillae. Tooth formation is abbreviated in *H. minuta*, at least for rows A-1 and P-2, and they can be considered vestiges even if the tooth ridges are well developed. Several authors (HEYER & CROMBIE, 1979; LANNOO et al., 1987; WASSERSUG, 1980; HEYER et al., 1990) refer to tiny or weakly developed teeth relative to tadpoles with dispersed or few labial teeth.

Conversely, the jaw sheaths of *H. minuta* are strong and well pigmented and keratinized, which suggests that they are efficient cutting instruments for harvesting large pieces of material by biting or ripping pieces from a substrate. The internal structure of the sheaths also supports this idea. Similar species may include *Hyla phlebodes* and *H. sarayacuensis* (WASSERSUG, 1980). The shape of the borders of the plant pieces found in the larval intestine of *H. minuta* indicates that they were cut with the jaw sheaths.

CONCLUSIONS

The labial teeth of *Hyla minuta* are short and weakly pigmented with a short basal sheath, and each tooth head has 3-5 sharp cusps. The tooth ridges have few columns of cells and each column produces few tooth generations. The development of labial teeth is abbreviated at least in some rows (A-1 and P-2).

Labial tooth rows have different tooth densities. Row A-1 has widely spaced teeth that may be distributed all along the tooth ridge. Row P-1 is well developed and most common with teeth distributed throughout the length of the tooth ridge. Teeth present in row P-2 row occur in sporadic patches of 3-5 teeth.

Judging from the anatomical features of the buccal cavity and oral apparatus of these tadpoles and their intestinal contents, I suggest that the tadpole of *Hyla minuta* functions as a herbivorous macrophagous feeder.

RESUMEN

Las observaciones del aparato bucal y de la cavidad oral de las larvas de *Hyla minuta*, efectuadas con microscopio óptico y electrónico de barrido, han revelado nuevos caracteres anatómicos para tomar en consideración. Las columnas formadoras de dientes (o columnas de células) de las hileras A-1 y P-2 son escasas. Cada columna presenta un número bajo de células epiteliales que darán desarrollo a los dientes córneos. Estos son cortos, sin cuello, y presentan poco pigmento. Cada espátula tiene de tres a cinco denticulos cortos y carenados, ubicados en el extremo distal. En el pico, las columnas formadoras de dientes están bien desarrolladas y muestran una acumulación de células cónicas en diferentes estadios de queratinización que refuerzan sus extremos y las paredes laterales. El pico superior es delgado y su extremo es filoso; el pico inferior es agudo y

presenta una posición proclive cuando se halla inactivo. Los dientes del pico tienen una cúspide. El desarrollo de los dientes labiales parece estar abreviado o incompleto, y no sería continuo durante la ontogenia. Cada hilera de dientes labiales puede presentar diferente densidad dentaria. La distribución de los mismos sobre los pliegues labiales de A-1, P-1 y P-2 puede estar incompleta o ausente en A-1 y en P-2. Las características de la cavidad oral son las siguientes: papilas del arena del techo y del piso de la boca altas y escasas, sin papilas linguales; velo ventral con proyecciones marginales reducidas; puentes lateral y medio presentes; fosetas glandulares en el velo dorsal y en la región posterior del techo bucal. En el contenido intestinal se hallaron algas perifíticas, grandes trozos de algas filamentosas, de cyperaceas (Cyperaceae), y de tejido meristemático, y gránulos de almidón, que permiten considerar a la larva de *H. minuta* con una tendencia trófica del tipo macrófago hervíboro, por lo menos en términos cualitativos. El pico córneo es el elemento del aparato bucal de *H. minuta* que tiene más importancia en la supervivencia de la larva.

ACKNOWLEDGMENTS

I am most grateful for the assistance from several people: Dra. Elena ANCIBOR, Laboratory of Vegetal Anatomy, University of Buenos Aires, for identifying plant material; Dr. Jorge WRIGHT, Laboratory of Mycology, University of Buenos Aires, for critically reading the typescript, Dr. Ronald ALTIG, Mississippi State University, for advice and comments, Lic. María F. ROCA, Department of Biological Sciences, University of Buenos Aires; Mr. Dante GIMENEZ, SEM Service of CITEFA, for technical assistance; and the Director of Administración de Parques Nacionales and staff of the Iguzú National Park for allowing me to capture the tadpoles for this study.

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Corresponding editor: Ronald G. ALTIG.